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THE EVOLUTION OF HERBACEOUS PLANTS AND ITS BEARING ON CERTAIN PROBLEMS OF GEOLOGY AND CLIMATOLOGY

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Evidence from living and fossil plants has often proved of value in geological investigations. A large part of our information as to the climate of the various regions of the earth during ancient times, particularly in the Mesozoic and Tertiary, has been derived from a study of the plants composing the various fossil floras with reference to the climatic conditions under which their modern representatives live. A gradual differentiation and refrigeration of climate in the north and south temperate zones since the close of the Cretaceous have been pretty clearly indicated by such investigations.[1] Botanical evidence, particularly that derived from a study of the distribution of living and fossil plants, has also been of value to the student of ancient geography in providing support for such theories as that of a closer connection between North America and eastern Asia just before the Glacial period; a recent elevation of the coastal bench in eastern North America; and a more or less intimate union between Australia, New Zealand, and South America in recent times by means of an antarctic continent or archipelago.

[1] There is, of course, ample evidence that similar periods of refrigeration have occurred earlier in the earth's history, notably in Cambrian and Permian times.

In fact, the builders of all the various hypothetical land bridges have used an abundance of phytogeographical data.

Botanical evidence which has heretofore been of use to the geologist, however, has been mainly derived from a study of *flora* rather than of *vegetation;* a study of the species, genera, and families which inhabited a region in past or present time and not of the various plant types which they represent. It is now possible, however, to supplement this evidence by an investigation of the habit of growth of the various elements in a flora, with especial reference to the relative proportions of herbs and woody plants, particularly among dicotyledonous angiosperms.[1] Data thus obtained derive their importance from the following facts which recent investigation seems pretty thoroughly to have established: (1) The earliest angiosperms were woody plants. (2) Herbs attained but very little prominence until the beginning of the Tertiary, since which time they have increased very greatly in number. (3) The gradual refrigeration of the climate of the temperate zones during the Tertiary, with the appearance of a well-marked winter season, seems to have been the factor responsible for the development of most herbs, which are plants well able to withstand cold winters, in the form of seeds or underground roots and stems. (4) This herbaceous vegetation, which reached its greatest development in the land mass of the north temperate zone, was thus composed of plants which were very hardy, agressive, and rapidly dispersed, and it consequently spread far and wide into other and warmer portions of the globe.

The evidence on which these conclusions are based may be summarized briefly as follows:

From paleobotany.—The vast majority of angiospermous remains, especially from the Cretaceous, are of plants whose nearest modern relatives are always trees or shrubs. In the Tertiary, especially the middle and latter parts of the period, remains of herbaceous plants are much more frequent. This geological evidence,

[1] The monocotyledons were apparently derived in very ancient times from the primitive dicotyledonous stock in adaptation to an aquatic habitat. They are almost entirely herbaceous, and their few woody forms are evidently recent rather than primitive.

however, cannot be regarded as entirely conclusive, since the delicate leaves of herbs are probably less readily preserved than are the tougher ones of most trees and shrubs. Among the lower orders, however, it is quite certain that the ancient fossil lepidodendrids, sigillarians, and calamites, for example, were woody plants, and that their modern representatives are all herbaceous.

From anatomy.—The most important anatomical difference between a woody plant and an herb lies in the degree of activity of the cambium. In the former group this tissue lays down a thick ring of wood which increases in size year by year. In the latter the woody ring is either very much thinner or, more frequently, is broken up into separate bundles. In such cases the so-called "interfascicular" cambium, opposite the gaps between the bundles, is much reduced or quite inactive; and in the bundles themselves the cambium is often merely vestigial. That such a discontinuous cambium is not the primitive type is shown by the fact that in various ancient groups which were just acquiring secondary growth (as shown by the structure of their fossils) the cambium always began as a perfectly continuous ring and did not arise from the union of isolated fascicular cambia.

Furthermore, in the vascular tissue of most herbs, medullary rays and wood parenchyma are poorly developed or absent. These structures, however, always characterize the more primitive types of angiosperm wood.

These two pieces of evidence point to the conclusion that the herbaceous stem has been reduced from a primitive woody one. This reduction has been accomplished by a marked decrease in the activity of the cambium, and in many instances also by an increase in the height and width of certain of the medullary rays, resulting in the breaking-up of the continuous woody ring into a series of bundles. In its general topography the stem of an herb resembles that of the young twig of its woody relatives.

From phylogeny.—It is generally admitted that the angiosperms have been derived either from the Bennettitales or from some stock derived from the Coniferales. There are no herbaceous forms in either of these groups. Among living angiosperms it is uncertain whether the nearly naked flowered Amentiferae or the complete

flowered Ranales and their allies are the most ancient members of the phylum, but the distinction in all probability belongs to one of these two groups. The Amentiferae are almost exclusively woody plants, as are the vast majority of the Ranales.

Evidence that herbaceous angiosperms are of comparatively recent origin is also presented by a study of families which possess both woody and herbaceous members and in which it is possible to determine, on floral or other evidence, the relative antiquity of the two types. In the Leguminosae, for example, the Mimosoideae and Caesalpineae are with very few exceptions trees or shrubs; and the Papilionatae, which seem clearly to be more recent than the other two groups, contain almost all the herbs in the family. In a number of other orders and families (Umbelliflorae, Violaceae, Polemoniaceae, Borraginaceae, etc.) and even in certain genera, notably *Potentilla*, the same fact may be observed. In practically every case where the phylogeny of a mixed group can be definitely established it is found that the woody members are more ancient in type than are the herbaceous ones.

Still further evidence pointing to the same conclusion is furnished by a general survey of the distribution of herbs among the families of the dicotyledons. Of the 240 families belonging to this group of plants listed in Engler's *Syllabus* (7th ed.), 121, or a trifle over 50 per cent, are entirely woody, whereas only 35, or 14 per cent, are entirely herbaceous. Eighty-four families, or 35 per cent, possess both woody and herbaceous forms. Of these 14 are rarely herbaceous and 18 rarely woody. Of the entirely herbaceous families, almost all are either parasitic, insectivorous, or water plants, or are monotypic, and hence can lay no strong claim to primitiveness. Practically all typical land herbs belong to families which have woody members, as well; but many more than half of the families possessing woody species (121 out of 205) include no herbaceous forms at all. Had the original type of angiospermous vegetation been herbaceous, it would be very improbable that over half of all the families should have lost their herbaceous members. If woody plants are primitive, however, we can easily see that herbs might have arisen in only about half of the families. These facts are especially significant

because in number of *species* herbs are fully equal to woody plants.

From phytogeography.—That the differentiation and refrigeration of climate in the temperate zones, particularly in the north temperate land mass, have been the chief factors in the development of herbs is indicated by the present distribution of these plants over the earth. In temperate regions, which are subject to winter temperatures considerably below freezing, from 75 to 85 per cent of the dicotyledonous plants are herbaceous in habit. In arctic and alpine regions, which are still colder, from 85 to 90 per cent or more of the dicotyledons are herbs. The relative proportion of the two types is precisely reversed in tropical countries and under climates where freezing never occurs. In such regions only from 25 (or less) to 40 per cent of the dicotyledons are herbs. Table I presents an analysis of the dicotyledonous vegetation in several typical temperate, arctic, alpine, and tropical regions.[1]

TABLE I

Region	Number of Species	Number of Herbs	Percentage of Herbs
Northeastern United States	2,280	1,748	76
Rocky Mountains	2,206	1,910	86
Ellesmereland	76	71	93
Great Britain	927	821	88
Germany	1,117	947	84
Switzerland	1,899	1,726	90
Iceland	221	200	90
Brazil	15,981	4,092	25
British West Indies	2,249	675	30
Tropical Africa	8,577	3,560	41
Java	3,188	867	27

This evident adaptation of herbs to life in regions subject to low temperatures at certain seasons makes it very probable that the advent of a cold winter has indeed been the chief factor responsible for their origin, for there is a fairly constant relation between the minimum winter temperature of a region and the proportion of

[1] In all of the tropical regions of which the floras are tabulated here, there are more or less extensive upland or mountain areas which possess a relatively temperate climate and hence a fairly high proportion of herbs. In the tropical lowlands in each case, however, only from 10 to 15 per cent of the dicotyledons are typically herbaceous.

woody plants in its flora. The advantages of the herbaceous habit in a temperate climate are obvious. The plant is able to complete its whole life-cycle during the summer season and to live through the cold winter either under ground or in the form of seeds. Plants which cannot resist cold are thus able to thrive in temperate regions. It is a noteworthy fact that families whose members have aerial stems which are generally able to withstand low temperatures—such as the Fagaceae, Betulaceae, Salicaceae, Caprifoliaceae, and, in fact, most of the woody families of temperate regions—have few or no herbaceous species, for they have been well able to get along without them.

The gradual refrigeration of climate probably first dwarfed and stunted the primitive arborescent vegetation, killing outright many of the more delicate types, such as the fig, laurel, and cinnamon (of which we find fossil remains almost within the arctic circle); and then, by continually killing back the whole year's growth of these stunted shrubs, it probably converted them gradually into perennial herbs. The annual herb, which starts from seed each year, is evidently a still more recent development.

The herbaceous type thus developed has usually proved very vigorous and adaptable. It is far superior to the woody one in the relative amount of seed which it produces; and the fact that its life-cycle from seed to seed is completed in only one or two seasons, rather than in the long period of years which is necessary with most trees and shrubs, allows it to become dispersed much more rapidly. Its ability to live through adverse conditions of drought, in the same way that it does through those of cold, gives it an advantage in dry regions, and many herbs seem to have arisen in these dry regions in adaptation to discontinuity in moisture alone.

It seems most probable that herbs have evolved in the temperate portions of the Southern Hemisphere and in mountainous, desert, and even tropical habitats all over the world. The majority of the important herbaceous genera, however, seem from their present distribution to have originated in the temperate land mass of the Northern Hemisphere. The ease of dispersal over wide areas and the consequently keen competition among a great variety of plants have resulted here in the development of an exceedingly hardy and

aggressive herbaceous flora. Most of the dominant and widely spreading plants of today, including practically all weeds, originally belonged to this northern herbaceous vegetation. These "Scandinavian" plants have taken advantage of every opportunity to become widely dispersed and to establish themselves in other parts of the world, with the result that in the temperate regions of the Southern Hemisphere, for example, there are well over two hundred genera and even fifty or more species which are identical with northern ones; and in practically all the south temperate floras more than half of the herbaceous genera either have their center of distribution in the Northern Hemisphere or are very common there. There are comparatively few southern genera, on the contrary, which have successfully invaded the North.

That the evolution of herbs has taken place for the most part since the close of the Mesozoic is indicated not alone by the fact that refrigeration of climate seems to date from that time but also from the following phytogeographical evidence. In the four great temperate land masses of the Southern Hemisphere (Australia, New Zealand, temperate South America, and South Africa) the endemic genera and the very characteristic families, which undoubtedly represent the most ancient element in the vegetation, are com-

TABLE II

	Total	Herbs	Percentage Herbs
Australia—			
Species of non-endemic genera	2,301	1,251	54
Species of endemic genera	4,024	677	17
New Zealand—			
Species of non-endemic genera	711	460	64
Species of endemic genera	315	109	34
Patagonia—			
Species of non-endemic genera	920	720	76
Species of endemic genera	667	320	48
South Africa—			
Species of non-endemic genera	3,298	1,929	55
Species of endemic genera	4,686	1,390	29

posed, in very large majority, of woody plants,[1] as shown in Table II. Most of the indigenous herbs, however, belong to genera, and often

[1] "Endemic" genera are those which are either strictly confined to the region in question or have only a very few species outside of it.

even to species, which are identical with those in northern latitudes, and are therefore in all probability recent immigrants.

The slight degree of endemism among these southern herbs is the more significant when we remember that such plants, from the brevity of their life-cycle, are likely to change much more rapidly than woody forms and hence would develop into endemic types in a shorter time. The notable uniformity of flora, too, over most of the globe during the Cretaceous, as shown by fossil evidence, renders it very improbable that, if herbs had been a dominant feature of the vegetation of that period, they would now be so uniformly absent from the ancient portion of the southern floras. The union of southern Africa with Eurasia in the Miocene and the union of South America with North America in the Pliocene evidently mark the periods of the herbaceous invasion of these two continents. Australia has apparently been sufficiently isolated from Asia since the Cretaceous so that land animals have been unable to enter it. The northern members of its flora, however, have doubtless effected their entrance by a migration, in comparatively recent times, over the Himalayas and along the East Indies. Had herbs been numerous in the latter part of the Mesozoic, when the connection of Australia with Eurasia was evidently much more intimate, the present vegetation of the island continent would certainly contain a much higher percentage of such plants. That the very early Tertiary flora of Australia included few if any herbs is made even more certain by the fact that although in all probability northern Australia and New Zealand were connected at that period by a land bridge, none of the northern herbs which entered Australia from the East Indies are now found in New Zealand; and we are obliged to infer that they had not then arrived in Australia.

The period at which herbs became an important feature of the north temperate vegetation and began to spread thence southward is therefore pretty clearly set at somewhere in the early Tertiary.[1] That herbaceous dicotyledons existed in the latter part of the Mesozoic, however, especially in mountainous regions, is most

[1] Recently discovered evidences of glaciation just at the close of the Cretaceous are of importance in this connection.

probable, but it seems equally probable that their great development did not take place until after the close of that epoch.

Such, in brief, is the evidence for believing that herbaceous angiosperms are comparatively recent in origin; that they have been developed most abundantly in the north temperate zone, mainly since the Cretaceous, as an adaptation to the advent of a winter season; and that they have spread thence over most of the other regions of the earth. Let us now see what conclusions of importance to geologists and climatologists may be drawn from a study of the origin and dispersal of these herbs.

In the first place the distribution of herbs in the north temperate zone provides us with evidence as to the climate of this area at the time of the last Glacial epoch.

As to what was the composition of the northern flora before the advance of the ice sheet we cannot be very certain, but there is reason to believe that a much higher proportion of woody plants flourished there than at present, indicating the existence of a climate devoid of extreme cold. Such an inference is based on the composition of that considerable body of related species and genera which are common to eastern North America and eastern Asia and which are nearly or quite absent elsewhere. Gray[1] was the first to suggest that these plants were the remnant of the widespread pre-Glacial boreal flora which had been forced south by the advance of the ice and had been exterminated almost everywhere save in these two regions, which were the only ones in warmer latitudes into which it had been able to escape. If this hypothesis is correct, as subsequent investigations seem to indicate, and if this group of plants is truly a fair sample of the pre-Glacial flora of the north, a study of its composition is of considerable interest. Gray has published a list of the genera and species of eastern North America which are absent in Europe but which are represented by identical or closely related forms in eastern Asia. This list comprises 142 genera of dicotyledons, of which 70 are woody or predominantly so, and 240 species, of which 128 are woody. The flora is thus just about equally divided between herbs and woody plants. From the greater hardiness of most herbs it is probable that they have

[1] A. Gray, *Scientific Papers* (1879).

suffered less by extinction than have the woody plants, and consequently that even more than 50 per cent of the original boreal dicotyledonous flora consisted of woody forms. This analysis would seem to indicate that previous to the glacial invasion the climate of the north temperate zone had, for a long time at least, been devoid of extremes of cold. We know from fossil evidence that in several regions during the Tertiary temperate genera, such as oaks and poplars, grew side by side with such tropical or subtropical types as the palm and fig; and it therefore seems reasonable to infer that the climate was a very equable one and devoid of extremes of heat as well as of cold.

More conclusive evidence, however, is at hand as to climatic conditions near the ice front during the actual period of the glacial invasion. The vegetation of the whole temperate zone at that time of course lost heavily by extermination, but this extermination must have been much more pronounced among woody plants than among herbs, owing to the greater ability of the latter to withstand cold and other adverse conditions. It is a significant fact that the present flora of Europe north of the Alps is decidedly more impoverished than is that of corresponding temperate North America, and that although in the latter region approximately 25 per cent of the dicotyledons are woody, in the former only from 10 to 15 per cent are so. This paucity of indigenous trees and shrubs in northern Europe is especially noteworthy since experiment has shown that many species of delicate and warmth-loving trees and shrubs will grow in England, France, and Germany which cannot stand the droughts and winters of the northern United States. In America, too, there are representatives of a considerable number of woody families which are now absent in northern Europe, many of which occur there as fossils. These facts are evidently to be explained by the much greater adversities suffered by the European flora during the Glacial epoch. In North America, especially in its eastern portion, the vegetation could easily migrate southward at the advance of the ice and return northward at its retreat. In northern Europe, on the other hand, the southward escape of the vegetation was blocked, and it was crowded against the Alps, the Pyrenees, and the Mediterranean, thus suffering

heavily by extinction. These same natural barriers have also prevented any considerable northward migration since the retreat of the ice. The vegetation of northern Europe today seems, therefore, to be descended directly from that remnant which was able to survive on the unglaciated portions of France, Germany, and England. We have already noted the fact that the percentage of woody plants in the dicotyledonous flora of northern Europe is amazingly low, being only from 10 to 15 per cent of the whole. This is really a percentage typical of alpine or northern regions. Indeed, the proportion of herbs in Switzerland today is but little higher than that in the adjacent lowlands. The alpine character of the northern European flora is further emphasized by the strong resemblance which it bears to that of the flora of the Rocky Mountains, for the two floras are composed of almost exactly the same families and include a host of identical genera and even a large number of identical species. In fact, the flora of the Rockies presents a much closer resemblance to that of Europe than does the flora of the eastern part of the continent.

If the flora of northern Europe is indeed typically representative of that which flourished near the ice front during glacial times, the proportion of woody forms within it affords us a valuable index as to climatic conditions during the height of the ice age. The facts seem to indicate that when the ice sheeet had reached its greatest extent the country in its immediate front was neither a barren arctic tundra, as has sometimes been supposed, nor covered with a luxuriant temperate vegetation; but that the climate in general resembled that of the lower portions of the Alps or the Rockies today, being cold enough in winter to kill off all but the hardiest trees and shrubs but not sufficiently cold to reduce the whole vegetation to the few perennial herbs and stunted shrubs which are characteristic of arctic regions today. Of course this evidence is of value only as indicating the climate during the *coldest* period of the ice invasion, just as the percentage of herbs in a flora is indicative of the minimum winter temperature of the region. As to the climate of the presumably warmer interglacial periods it tells us nothing.

This conception of the dicotyledonous herb as a comparatively recent type of plant which has been developed extensively in the north temperate zone during the Tertiary and has spread thence far and wide over the globe also leads us to some interesting geographical conclusions. Those regions, such as southern Asia and Mexico, which have been invaded, at least in their more temperate portions, by a flood of northern herbs, have in all probability had a nearly or quite continuous land connection with northern Eurasia or North America during Tertiary time. Other regions, such as Australia, New Zealand, South America, and South Africa, where there is a markedly smaller percentage of herbs in the vegetation, have apparently had a much less intimate connection with the great land mass of the north temperate zone during the Tertiary. This is particularly true of certain oceanic islands, notably Hawaii, the Polynesian group, Juan Fernandez, the Canaries, St. Helena, Socotra, Mauritius, and the Seychelles, on which the percentage of herbs is much smaller than on the adjacent mainland. In these insular floras practically all the herbs belong to species which also occur on the near-by continent; and almost the entire body of the endemic genera, presumably the most ancient portion of the flora, is composed of woody plants, as is shown in Table III.

TABLE III

	Total	Herbs	Percentage Herbs
Hawaii—			
Species of non-endemic genera	339	117	34
Species of endemic genera	243	21	8.6
Fiji—			
Species of non-endemic genera	543	81	15
Species of endemic genera	20	0	0
Juan Fernandez—			
Species of non-endemic genera	57	27	47
Species of endemic genera	17	0	0
St. Helena—			
Species of non-endemic genera	34	15	44
Species of endemic genera	7	0	0
Mauritius and the Seychelles—			
Species of non-endemic genera	524	191	36
Species of endemic genera	63	3	4.7

This paucity of herbs, particularly of annuals, on oceanic islands was noted long ago by Darwin, Hooker, and others, and was ex-

plained (by Darwin[1]) as due to the fact that the lessened competition between the members of an insular flora allowed many plants to grow there into shrubs and trees which on the mainland could never succeed in attaining more than a herbaceous stature. From what we have seen as to the evolution of herbs this explanation appears inadequate, and it implies that, in many cases, herbs must have lost their great advantage of being able to pass from seed to seed in a single season. Insular floras appear rather to be relics of the ancient Tertiary vegetation which once flourished on the adjacent mainlands but which has been more or less superseded there by an influx of new plants, most of them herbs. The many striking differences in flora between Juan Fernandez and adjacent Chile; the Canaries and adjacent Morocco; St. Helena and adjacent South Africa; and Socotra and adjacent Somaliland seem to point to this conclusion. Strongly in favor of such a view are also the very numerous floral resemblances exhibited between distant islands or between islands and distant continents. The occurrences of shrubby species of Plantago only in Hawaii, Juan Fernandez, and St. Helena; of phyllodineous Acacias only in the Mascarene region, Hawaii, and Australia; of related shrubby Compositae in Hawaii, Tahiti, the Galapagos, and Juan Fernandez, and of numerous related species in the Canaries, South Africa, and Socotra constitute a few of many instances of such distribution. The very large proportion of woody plants compared to herbaceous plants in these insular floras and the high degree of endemism of the former as opposed to the latter strongly favor the theory that these particular islands do indeed support a very ancient type of organic life, and that since the opening of the Tertiary at least they have not been intimately connected with any large continental area.

Other isolated islands or archipelagoes, such as Bermuda and the Azores, possess as high a percentage of herbaceous plants in their vegetation as do the adjacent continental areas, and they likewise have a very small endemic element. We are forced to conclude, on evidence both from the flora and from the composition of the vegetation, that such islands have appeared, or at least have received their plant life, in comparatively recent times.

[1] C. Darwin, *Origin of Species*, 6th ed., p. 413.

Aside from its bearing on the antiquity of oceanic islands and other isolated regions, the present theory as to the origin and dispersal of herbs is of importance as indicating the conditions under which occurred that momentous botanical event of the Tertiary—the invasion of the Southern Hemisphere by a flood of northern plants. Phytogeography indicates that this invasion took place along three main routes: over the Andes into Patagonia and thence over an extensive antarctic continent or archipelago into New Zealand and southeastern Australia; over the central African highlands into South Africa and Madagascar; and over the Himalayas and along the East Indies into Australia. These invasions seem to have ceased entirely at the present time, for there are in most cases wide gaps of hundred or even thousands of miles between the northern and the southern ranges of a genus or a species. That the immigration into Africa and Asia ceased some time ago is indicated by the fact that in these continents there are now almost no species identical with northern ones, although the genera are still the same. The highway over the Andes, however, seems to have closed much more recently, for there are a large number of species which traversed it that are still identical with their boreal types. The significant facts in this connection are that, with the exception of a very few genera which are poor in species, this invasion by the "Scandinavian" flora was an invasion of *herbs*,[1] and that herbs are peculiarly adapted to temperate climates. This immediately suggests the conclusion either that these three mountain highways were considerably more elevated during the Tertiary, with a consequent increase in the extent of temperate areas (a

[1] The presence of such temperate types as Betula, Populus, and Quercus in the Cretaceous of Patagonia, as described by F. Kurtz ("Contribuciones a la palaeophytologia Argentina—Sobre la existencia de una Dakota flora en la Patagonia austro-occidental," *Revista museo la plata*, X [1899], 1902, pp. 43–60), and in the Cretaceous and even Tertiary of Australia and New Zealand by Baron C. von Ettinghausen ("Tertiary Flora of Australia," *Gov. Surv. N.S.W. 1888*, p. 82; "Contributions to the Knowledge of the Fossil Flora of New Zealand," *Trans. New Zealand Inst.*, XXIII [1890], 237) (the latter's identifications are often open to grave question, however) has probably nothing to do with the Tertiary invasion of herbs but rather bears witness to the remarkable uniformity and intermingling of the Cretaceous flora. Had these ancient temperate plants been accompanied by anything like the throng of herbs which now surrounds them in the north, it is highly improbable that herbaceous forms would now be so scarce in the south temperate zone. Because of the brevity of their life-cycle, herbs are likely to change very rapidly, and the slight degree in which these "northern" herbs in the antipodes have become altered also bears witness to their comparatively recent arrival.

hypothesis which the Tertiary origin of the Andes and Himalayas may perhaps be regarded as supporting); or that for some other reason, possibly an increase in glaciation, the area of regions enjoying a cool climate in the tropics has at various times been considerably augmented.

In this connection it is of interest to note the evidence which is accumulating as to the occurrence of more or less widespread glaciation both at the transition from Cretaceous to Tertiary and again during the Miocene. It is possible that the more ancient herbaceous invasions were coincident with these earlier glacial periods and that the later migration of such plants into the antipodes was contemporaneous with the extensive glaciation which marked the latter part of the Tertiary.

The theory put forward by Hackel[1] and supported by Scharff[2] asserts that the boreal plants in antipodean South America are extremely ancient types which have preserved their specific identity for an exceedingly long time; that they migrated over a land bridge long since destroyed; and that instead of having come south along the Andes they are at present going north. Such a theory is certainly not tenable if herbs are proven to be of recent origin. The increasing frequency of northern herbs as one goes south along the Andes, the fact on which Hackel's hypothesis is based, is well explained by a decrease in temperate areas within the tropics as by a migration from the south. It is also very difficult to imagine so many forms maintaining or almost maintaining their specific identity for such a very long period of time. The present theory of the origin of herbs certainly supports the view that they have entered the antipodes rather recently over land bridges which have not had time to become fundamentally altered.

We have already spoken of the antarctic continent as a highway between South America and Australasia; and the existence in comparatively recent times of such an extended Antarctica, able to support a large fauna and flora, has been postulated by almost all students of the distribution of antipodean plants and animals.

[1] E. Hackel, "Über die Beziehungen der Flora der Magellansländer zu jener d. nördl. Europa und Amerika," *Mitteil. naturw. Verein Steiermark* (Botan. Sekt.) (1905), pp. 110–15.

[2] R. F. Scharff, *Distribution and Origin of Life in America* (1912), p. 418.

That during its greatest extent, however, it was probably not a continuous land bridge but more in the nature of a great archipelago, presenting a barrier to most animal invaders but much more easily crossed by plants, seems to be generally admitted. It is worth our while to analyze the ancient "endemic" flora of this antarctic continent and archipelago and to find, if we may, what the climatic conditions were under which it flourished. It seems to be a reasonably safe conclusion that all genera commonly designated as "antarctic," from their confinement to the temperate regions of the Southern Hemisphere, were once inhabitants of Antarctica. The writers have compiled a list of eighty-eight dicotyledonous genera which have representatives in at least two of the three main antarctic regions—New Zealand, Australia, and temperate South America—and which possess but very few species outside these regions. This list may well be regarded as representative of the flora of Antarctica (except for the northern invaders) before the advent of the cold period which drove the phanerogamic vegetation northward into South America and Australasia. Of these eighty-eight genera only thirty-four, or 38 per cent, are typically herbaceous. These few herbs are obviously unrelated to northern ones and seem clearly to have had an independent origin in the antipodes in response to the refrigeration of the climate. That they are not as ancient as the northern herbs appears to be indicated by the fact that the annual type has not yet been evolved among them. If the northern invasion which crossed Antarctica did not enter it until the Pliocene (as seems probable), no very extreme refrigeration could have taken place until the latter part of that period, at any rate. The very high percentage of woody plants in the original flora, however, seems to testify strongly to the existence in Antarctica at no very ancient date of a climate devoid of extreme cold. The refrigeration of this climate and the evolution of its herbaceous vegetation, instead of being the slow and gradual processes that they were in the Northern Hemisphere, seem to have been much more rapid. The consequently scanty number of herbs and the lack of time or space for very vigorous competition among them doubtless explain why the antarctic herbs are not as widespread and aggressive as their northern congeners.

Such are the more important geological and climatological inferences to which we are led by a recognition of the recent and predominantly boreal origin of herbs, and of the factors which have determined their origin. Much more complete data must be sedulously gathered, particularly by the phytogeographer and the botanical phylogenist, before the full application of this theory to the problems of geology can be definitely determined. That it is possible, however, to draw conclusions of importance to geology and climatology, not alone from the past and present distribution of species, but also from a study of the evolution of the growth of habits of plants, will be readily admitted.[1]

SUMMARY

1. The earliest angiosperms were woody plants, and herbs have been derived from them by reduction. This is indicated by the facts that: (1) the earliest angiosperm fossil remains are almost entirely of woody plants; (2) the uninterrupted and active cambial ring of woody dicotyledons, which lays down secondary wood provided with well-developed medullary rays and wood parenchyma, is the primitive type and that the much reduced secondary tissues in herbs are clearly derived from this; (3) the ancestors of the angiosperms and the great majority of the primitive members of the phylum are woody plants; and that (4) in all families and genera which contain both woody plants and herbs the latter are more primitive in their constitution.

2. The differentiation and refrigeration of the climate of the temperate zones since the beginning of the Tertiary, and the consequent appearance of a cold winter season, have been the chief factors which have caused the evolution of herbs. Herbs are able to survive adverse conditions of temperature or moisture as underground roots and stems or in the form of seeds, and can thus thrive in regions where plants with perennial aerial stems would perish. In general, the lower the winter temperature of a region the fewer the woody plants in its flora.

3. At least half of the pre-Glacial vegetation of the north temperate zone seems to have been composed of woody plants,

[1] A more complete discussion of the present problem with the presentation of a much larger body of data will be found in a paper by the writers, "The Origin and Dispersal of Herbaceous Angiosperms," *Annals of Botany*, XXVIII (1914), 547–99.

indicating the occurrence of a rather mild winter. The advent of the Glacial period resulted in very great extermination of the flora, but herbs suffered much less than did woody plants.

4. In America the vegetation was able to return northward after the retreat of the ice and thus shows a considerable proportion of woody species today. In northern Europe, however, natural barriers have to a great extent prevented this return, and the present flora of that region seems to be descended from the remnant of the pre-Glacial vegetation which survived on the unglaciated areas. The fact that the proportion of herbs in the present north European flora is like that in northern or low alpine regions today provides us with a clue as to climatic conditions during the height of the glacial invasion.

5. The land mass of the north temperate zone has been the seat of origin of a very large part, if not of the majority, of herbaceous genera. The opportunities for wide dispersal and keen competition here have resulted in the production of a very hardy and aggressive herbaceous flora which has spread widely into the tropics and the Southern Hemisphere.

6. This invasion of herbs from the north has taken place for the most part during the Tertiary, and the percentage of herbs in the floras of the various regions in the tropics and the Southern Hemisphere indicates roughly the intimacy of the connection between these regions and the land mass of the north temperate zone during Tertiary time. The floras of certain oceanic islands, for example, seem from the extreme paucity of herbs to be very ancient in type, implying a very long period of isolation; whereas the floras of other islands, overwhelmingly herbaceous, indicate a recent origin for these islands or at least for their plant populations.

7. Boreal herbs in the antipodes are usually separated from their northern congeners by considerable distances, indicating that migration has ceased and that the wide area of rather temperate climate within the tropics, under which the invasion took place, has recently become much smaller.

8. A reconstruction and analysis of the ancient flora of the antarctic continent indicate that up to comparatively recent times its climate was very mild and that refrigeration took place more rapidly than in the north temperate zone.